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FORAGING AND HABITAT RELATIONS OF INSECTIVOROUS BIRDS IN A MANAGED SIERRA NEVADA MIXED CONIFER FOREST

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Foraging and Habitat Relations of Insectivorous Birds in a Managed Sierra Nevada Mixed Conifer Forest

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FORAGING AND HABITAT RELATIONS OF INSECTIVOROUS BIRDS IN A MANAGED SIERRA NEVADA MIXED CONIFER FOREST

Daniel Anthony Airola

ABSTRACT

The foraging behaviors and substrates used by 12 breeding insectivorous passerines in a Sierran mixed conifer forest are described. The objectives of the study were: (1) to determine the degree of preference shown for different tree species and foliage heights by foraging birds, (2) to compare their use of foraging substrates and techniques, and (3) to compare the distribution of breeding territories over the forest. Many of the species showed selectivity in use of foraging substrates, but species differed considerably in their preferences for tree species and height classes. When data for all birds were pooled, the pattern of foliage use corresponded closely to that available at different heights except below 2 m. In contrast, the community showed striking non-random use of tree species, preferring ponderosa pine, sugar pine, white fir and black oak but avoiding incense cedar.

Comparisons of overlap in foraging substrates and foraging behaviors showed the latter to be more important for ecological segregation. Species were compared for similarity in foraging methods (heights, trees, and behaviors) and geographic distribution. A correlation of overlaps on these two axes showed no relationship. Thus the hypothesis that interspecific competition is presently important in structuring the community as a whole during the breeding period is not supported by the available data. However, it is possible that competition may contribute

to the observed foraging and distributional patterns of certain guild members.

Potential impacts of forest management practices on the 12 birds are discussed, in light of their observed foraging substrate preferences.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

Acknowledgements i

Table of Contents ii

List of Tables iv

List of Figures v

Introduction 1

Methods

Study Area 2

Data Collection

Sample Plots 4

Foraging Data 4

Vegetation Sampling 7

Analysis 8

Results and Discussion

Foraging Height 11

Tree Species 17

Foraging Behavior 24

Niche Breadth 27

Niche Overlap 29

Distributional Overlap 38

Foraging and Distributional Overlap 42

Conclusions

Limitations of the Study 47

Topics for Future Research 48

Management Applications 51

Summary 53

Literature Cited 55

LIST OF TABLES

1. Summary of preferences by 12 insect-gleaning bird species for tree species used in foraging at Blodgett Forest. 22

2. Niche breadths for foraging heights, tree species and foraging behaviors of 12 insect-gleaning birds. 28

3. Results of correlations of foraging niche breadths for pairs of species on 3 niche axes. 30

4. Pairwise overlap values for insect-gleaning birds on 3 foraging niche axes (foraging height, tree species and foraging behavior), the product of the three overlap values and mean overlap values for each species. 31

5. Results of correlations of foraging niche overlaps for pairs of species on 3 niche axes. 33

6. Pairwise overlaps of 12 insect-gleaning birds based on frequency of occurrence on 41 sample plots. 39

LIST OF FIGURES

1. Foraging height class preferences of the insect-gleaning guild at Blodgett Forest. 12

2. Foraging height class preferences for each of the 12 insect-gleaning guild members. 14

3. Tree species preferences of the insect-gleaning guild at Blodgett Forest. 18

4. Tree species preferences for each of the 12 insect-gleaning guild members. 20

5. Foraging behaviors used by individual birds and the insect-gleaning guild as a whole. 25

6. Dendrogram of similarity in uses of foraging methods by the 12 species. 36

7. Dendrogram of similarity in geographic association of the 12 guild members based on their frequency of occurrence on 41 sample plots. 40

8. The relationship between overlap in foraging method and geographic distribution for each combination of insect-gleaning species pairs at Blodgett Forest. 45

INTRODUCTION

Within a community bird species subdivide the spectrum of available resources, presumably as a result of evolutionary pressures to increase foraging efficiency and reduce competition. For insectivorous birds, food is considered by many to be the primary limiting factor on which communities are structured (Morse 1971, Hespenheide 1975), although others disagree (Hilden 1965). Because of the immense difficulty of measuring insect food abundance, most studies have used habitat use as an index of food use. Methods of habitat partitioning by birds foraging for insects include selection of: (1) different foraging heights (MacArthur 1958, Balda 1969, Cody 1974); (2) tree species (Hartley 1953, Morse 1976a, Balda 1969, Franzreb 1978); (3) positions within tree crowns (MacArthur 1958, Morse 1967b); and (4) foraging actions (Root 1967, Sturman 1968).

Application of these ecological principles to management concerns is essential to determine the influence on wildlife of large scale vegetation manipulation by timber managers. Accurate predictions of the impacts of management actions on birds can most readily be made when the bases for habitat selection by individual species and community relations of species are known.

The objectives of this study were: (1) to describe the preferences shown by 12 insect-gleaning birds for vegetation heights, tree species and behaviors used in foraging in a mixed conifer forest; and (2) to compare the patterns of resource use by these birds to investigate the mechanisms of ecological segregation within the community.

METHODS

Study Area

Blodgett Forest Research Station comprises 1,186 hectares of mixed conifer-oak forest managed by the Department of Forestry and Resource Management, University of California. It is located on the west slope of the Sierra Nevada in Eldorado Co., mainly between 1350 and 1450 meters. Topography is gentle; slopes of 50% are uncommon, while much of the forest has slopes of less than 20% (Zinke et al. 1965).

The climate at Blodgett Forest is a modified Mediterranean type, characterized by warm, dry summers and mild, wet winters. Weather data have been collected on the Forest since 1962. Average precipitation is 170 cm, including 33 cm water equivalent as snow, but yearly variation is high (coefficient of variation = 20%). The average frost free season is 186 days.

Four distinct soil types are recognized at Blodgett Forest. Three are derived from a grano-diorite parent material and one is from an andesite. Soils are generally heavily weathered, often to depths of 1.6 m or more (Zinke et al. 1965).

The mixed conifer forest (Rundel et al. 1977:563) occurs as an elevational zone distributed along the west slope of the Sierra Nevada, from approximately 1250-2200 m. The major tree species, listed in order of decreasing abundance in the study area are: incense cedar (Libocedrus decurrens), white fir (Abies concolor),

Douglas fir (Pseudotsuga menziesii), California black oak (Quercus kelloggii), ponderosa pine (Pinus ponderosa) sugar pine (Pinus lambertiana), and tanoak (Lithocarpus densiflora). Major shrubs include (Ceonothus integerrimus, C. cordulatus, Arctostaphylos patula, A. viscida, Ribes roezlii, Chameabatia foliolosa and Castenopsis chrysophylla var. minor. Common forbs include Trientalis latifolia, Goodyera oblongifolia, Iris hartwegii, Viola lobata, Galium sp. and Collomia sp.

All of Blodgett Forest was logged and subsequently burned between 1900 and 1913, resulting in the removal of nearly all large pines and some firs. Much of the present forest has naturally regenerated following this disturbance. Except for a fire that burned through the south end of the forest in 1919, other major disturbances have resulted only from silvicultural manipulations.

The present vegetation consists of a mixture of all major species resulting from their differing tolerances for light and soil moisture. Following creation of large openings in the forest canopy, forbs and brush establish and quickly dominate. Also during this phase the pines, and to a lesser extent Douglas fir, regenerates and eventually grow to dominance. In contrast, white fir and incense cedar characteristically regenerate at the edges of openings and under the sparser canopies of the overstory trees. While frequent low intensity fires formerly reduced this understory in pristine times, fire exclusion in this century has resulted in the accumulation of these species in many areas (Rundel et al. 1977:560). These shade tolerant understory trees are released through natural mortality or harvesting of individual

overstory trees. They have become dominant over much of Blodgett Forest.

Although acquired by the University of California in 1933, intensive forest management began at Blodgett Forest in about 1960. The Forest is divided into management compartments of 5 to 20 hectares. Compartments are evenly allocated to three silvicultural regimes: (1) even-aged management, (2) uneven-aged management and (3) no manipulation. At present, approximately half of the compartments scheduled for management have been manipulated. Current silvicultural practices affecting avian habitats include: clearcutting, group and individual tree selection, planting of seedlings, spraying and mechanical control of brush, thinning of dense forest stands and road building.

Data Collection

Sample plots -- Between 10 May and 7 July 1977, a random set of 41 plots was sampled from a previously established 100 point random plot system designed for timber inventory. Bird abundance was recorded for all species present on a 0.28 hectare circular plot during each of 20 consecutive 10 minute intervals, beginning one half hour after sunrise. Frequency of occurrence served as the measure of abundance.

Foraging data -- Foraging behaviors and use of substrates by birds were recorded on and near plots during bird frequency counts and in walking transects in varied locations around the Forest. Hours of observation were generally from sunrise to 10:30 and 16:00 to 19:00, the periods of greatest activity. These data were collected from early May to early July in 1977 and 1978.

Three niche dimensions, or resource axes, were considered: foraging height class, tree species and foraging behavior. Foraging height was recorded in the following height classes: 0-1 m, 1-3 m, 3-7 m, 7-20 m, 20-35 m. Of all plants occurring in the study area, only the six major tree species (ponderosa pine, sugar pine, white fir, Douglas fir, incense cedar and California black oak) are analyzed for plant species use. These were the dominant plants, and were used almost exclusively by the birds considered here. Tanoak was eliminated from analysis because of its sparcity and low use by birds. Foraging behaviors were recorded during 1978 only, and included the following (after Root 1967 and Sturman 1968): (1) hawking (flying from a perch to take aerial insects); (2) hovering (taking insects from foliage while in flight; (3) lunging (leaping from a stationary position to take insects moving within the crown); (4) foliage gleaning (taking objects from foliage while perched); (5) twig (<1 cm diameter) gleaning; (6) branch (>1 cm) gleaning; (7) spider web use; (8) sapsucking (from drillings of Red-breasted Sapsuckers, Sphyrapicus varius ruber), (9) trunk gleaning, and (10) trunk excavating (removing wood to get at insects).

The foraging behaviors described above combine two classes of information: (1) the position of the bird in the crown of the tree (aerial, foliage, twigs, branches and trunk), and (2) the technique or "foraging tactic" (Root 1967) at that position. These were combined because they are partially dependant on one another. For example, hovering and lunging invariably occurred in foliage, while sapsucking

and excavating almost always occurred on tree trunks. When niche dimensions are dependant, it is best to combine them into a single measure that does not duplicate information (May 1975, Inger and Colwell 1977).

Multiple observations of individuals were recorded to increase sample sizes and more importantly to reduce biases for lower foraging heights and more open foliage which may have influenced my ability to locate birds. Once a bird was located, later observations were less affected by these biases. I assume that because a large number of individuals and locations were sampled, multiple observations did not unduly bias a species' use pattern for a particular individual's preferences or the vegetation characteristics in a local area.

Sample sizes for different variables differ within a single species because more than one height class may have been recorded in a single tree and more than one technique used at a single height. Nevertheless, because foraging techniques were recorded only during 1978, they show the smallest sample sizes.

Of 70 bird species known to occur at Blodgett Forest, 12 of the most common members of the insect-gleaning guild (Root 1967) are analyzed in this study. All are passerines. They include the: Mountain Chickadee (Parus gambeli), Chestnut-backed Chickadee (Parus rufescens), Red-breasted Nuthatch (Sitta canadensis), Brown Creeper (Certhia familiaris), Golden-crowned Kinglet (Regulus satrapa), Solitary Vireo (Vireo solitarius), Warbling Vireo (Vireo gilvus), Nashville Warbler (Vermivora ruficapilla), Yellow-rumped Warbler (Dendroica

coronata), Hermit Warbler (Dendroica occidentalis) Western Tanager (Piranga ludoviciana) and Black-headed Grosbeak (Pheucticus melanocephalus).

Vegetation sampling -- Vegetation measurements were made on census plots in conjunction with an ongoing study of the impacts of silvicultural practices on local vertebrates. Twenty circular 10 ca subsamples were situated in a radial pattern on the bird census plots. Plant species composition and vertical structure of the vegetation were the major classes of variables sampled.

Species composition was determined by visually estimating percent canopy cover on each subsample element for each plant species independantly (Mueller-Dombois and Ellenberg 1974:63). Thus, the total plant cover sometimes exceeded 100%. Mean cover values per plot were calculated from element cover values. Plot means were averaged to derive a grand mean for the whole forest. The proportion of the grand mean contributed by each of the 6 major tree species was considered as the proportion available for use by birds.

Vertical structure of the vegetation was determined by estimating the total cover (all species combined) in each of eight height classes: 0-0.5 m, 0.5-2 m, 2-5 m, 5-10 m, 10-15 m, 15-20 m, 20-30 m, and 30-40 m, on each element. The maximum value for any height class could not exceed 100%. As in species composition measures, elements were averaged to obtain plot means, and plot means were used to derive a grand mean for cover in each stratum. The proportionate contribution of each height class to the sum of the grand means was the proportion available in each class for use by birds.

Analysis

Foraging observations were summmarized for tree species and vertical height categories with the SPSS subroutine CROSSTABS (Nie et al. 1970). Because the height classes used in recording vegetation and bird foraging were different, diagrams of the vegetation height use profiles were transformed graphically to the same classes as recorded for vegetation.

The strength of preference for a height class or plant species was described by Ivlev's (1961) forumula: $O_{ij}-E_{ij}/O_{ij}+E_{ij}$. Where O_{ij} is the frequency of observation of bird species i in height class or tree species j, and E_{ij} is the expected frequency of bird i in height class or tree j based on the proportion of foliage j available, taken from the height strata or vegetation cover proportions, respectively. The resulting preference values are bounded by -1 and +1 with negative values indicating avoidance, zero showing use equal to availability, and positive values indicating positive selection. The magnitude of the index values describes the strength of the selection or avoidance shown, although there may be inheirant biases in the values, making comparisons between studies risky (Strauss 1979).

In calculating preferences for the insect-gleaning community as a whole, use proportions were derived by weighting each individual species' proportions by its relative abundance in the 1977 random plot census, summing the weighted proportions and re-calculating community use proportions based on this sum. This weighting was considered to be the best way to describe the whole community since the relative abundance

of a species' foraging observations in the raw data was biased to some extent by an attempt to get equal sample sizes.

Differences between observed and expected use of tree species and height classes were tested for significance with a X^2 test with 1 d.f. at $p < .05$. When use exceeded or was less than availability, selection or avoidance was shown respectively.

Niche breadths and overlaps in foraging heights, tree species, foraging techniques and geographic distributions on sample plots were calculated by the Colwell and Futuyma (1971) method using non-circular niche metrics and relative weighting factors for resource states. This method corrects for the arbitrariness of resource state definition by using all other members of the community as an ecological assay of resource state distinctness, and applying a correction factor to resource states based on their calculated distinctness. Niche breadth values are expressed as the proportion of the maximum value for each axis. This permits comparisons of different axes by scaling the breadths to the same range.

Cluster analysis was accomplished with the NTPAK program (Beverino and Swanson 1976), grouping species on the basis of their degrees of similarity in: (1) foraging overlaps, and (2) co-occurrence on sample plots. The Colwell-Futuyma overlap measures were used as the similarity functions for clustering. Groups were combined on the basis of the average similarity of all existing group members. This procedure results in a graphical representation of the similarity of species based on their overlaps in foraging and distribution.

To show the relationship between the overlaps of species in foraging methods and their degree of geographic association, a correlation analysis of these overlap values was performed using the SPSS subprogram SCATTERGRAM (Nie et al. 1970). A positive correlation would suggest a lack of habitat segregation by species that are similar in foliage heights, tree species, and foraging behaviors used. A negative correlation would suggest that similarly-foraging species tend to segregate geographically.

RESULTS AND DISCUSSION

Foraging Height

Preference values for the 8 foliage height classes by all 12 species combined are shown in Figure 1. For this community, the upper 6 foliage layers are not used in a manner significantly different from that expected if use was proportional to foliage available in each height class. The lower two foliage layers were selected against by these birds.

When the birds are considered individually, considerable variation in foraging height preference is evident (Figure 2). In general, those species that specialize on foliage prefer upper height classes, while branch and trunk specialists prefer lower strata (compare with Figure 5).

Among individual species, no significant differences in proportions of used and available foliage in different height classes could be shown statistically, although preference values were strongly negative for most species in the lower two foliage height layers. This lack of any significance stems at least in part from the transformation of the height use classes to foliage availability classes which tends to make adjacent height class proportions more similar than they actually are.

That 11 of the 12 species show a negative preference value for the 0-0.5 and 0.5-2 meter height classes is probably explained by two considerations. First, these lower foliage layers include many brush

Figure 1 - Foraging height class preferences of the insect-gleaning guild. Each species' contribution to the guild is weighted by its relative abundance on bird frequency sample plots. Each dot represents the mid-point of a foraging height class. Open circles designate height classes in which used and available proportions differed significantly (χ^2, 1 d.f., $p < .05$).

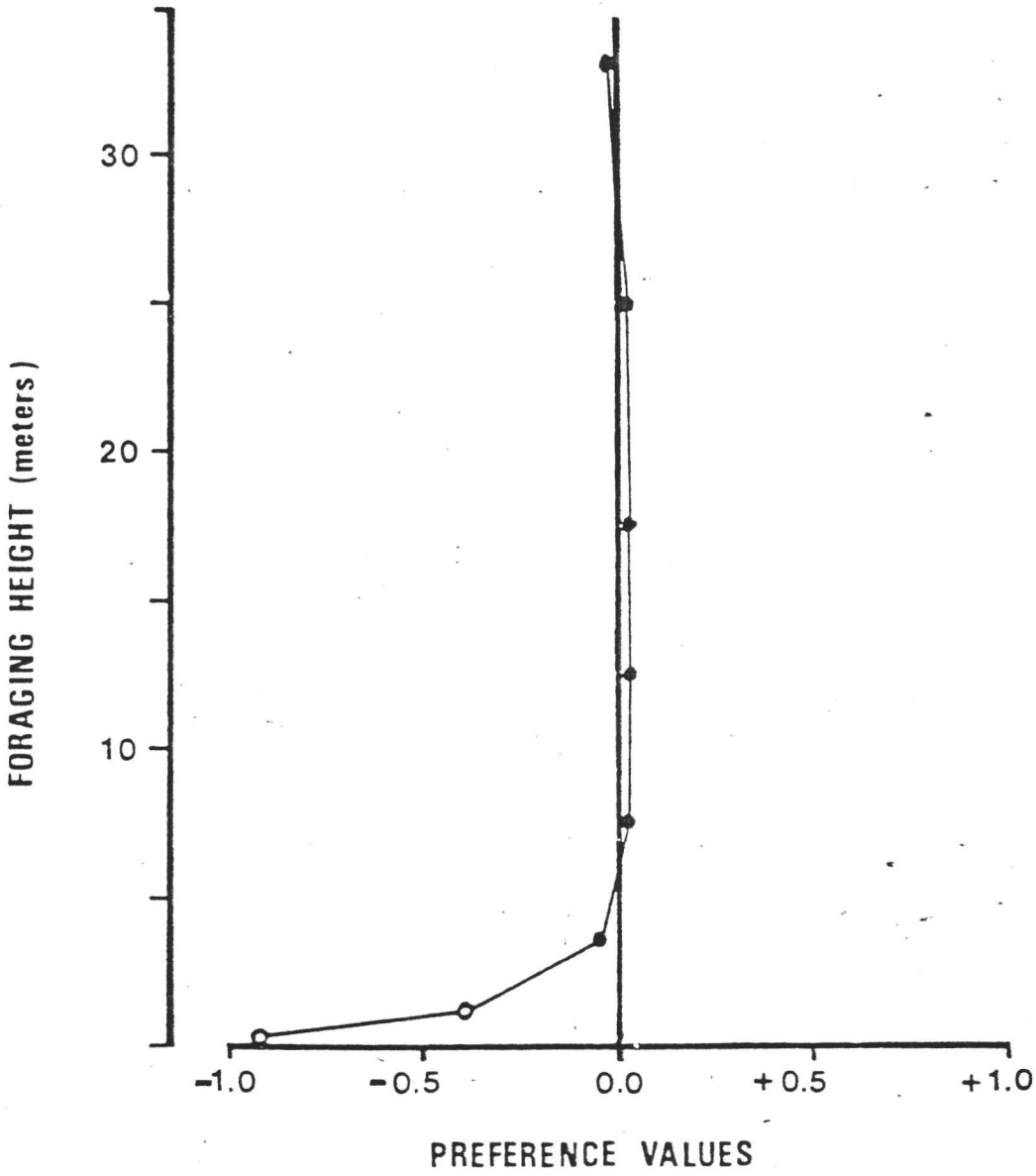
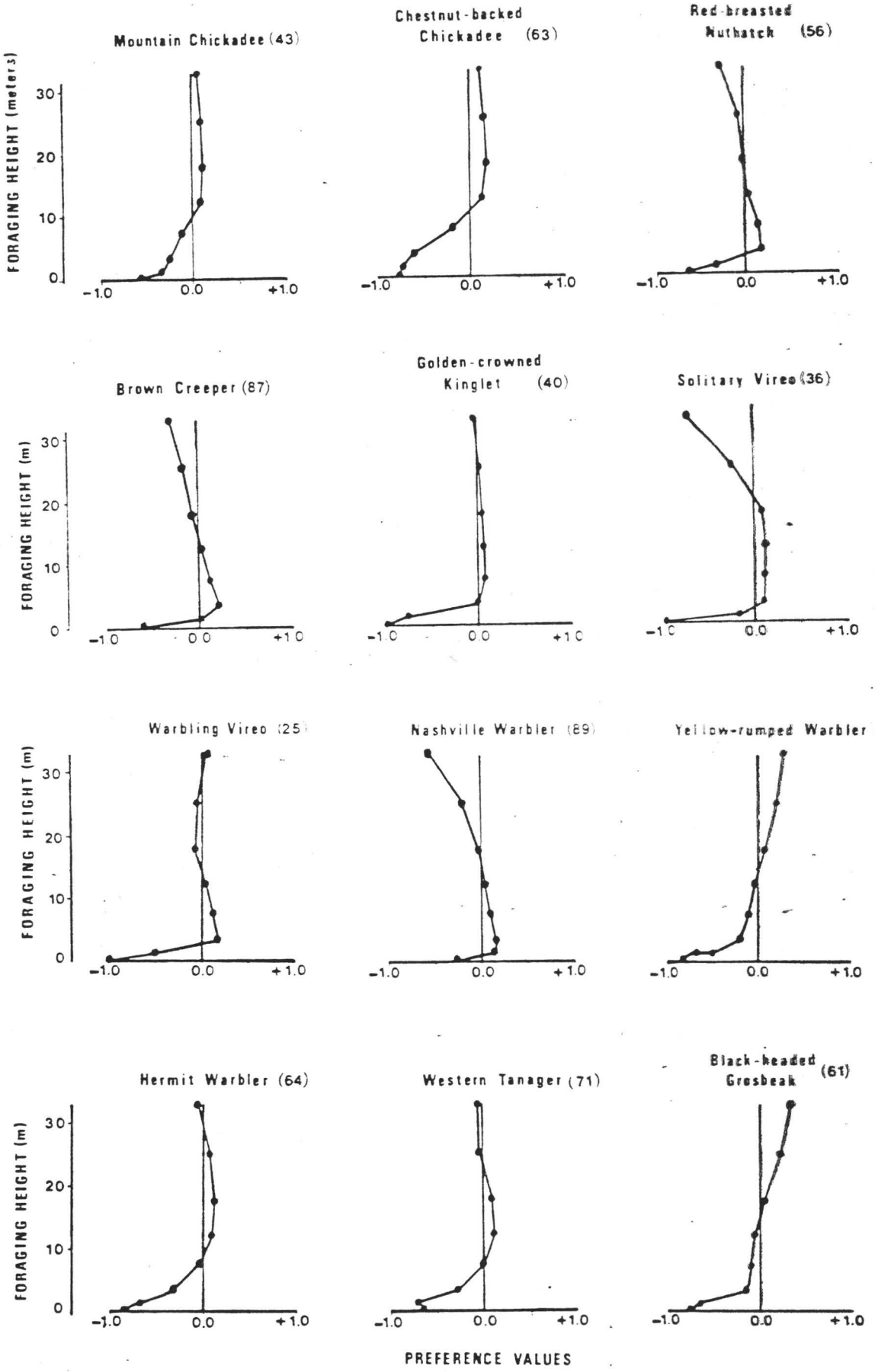

FORAGING HEIGHT (meters)
30
20
10
-1.0
-0.5
0.0
+0.5
+1.0
PREFERENCE VALUES

Figure 2 - Foraging height class preferences (Ivlev 1961) of species in the insect-gleaning guild taken during the breeding season. Each dot represents the mid-point of a foliage height class. Numbers of observations are shown in parentheses.


Mountain Chickadee (43)
Chestnut-backed Chickadee (63)
Red-breasted Nuthatch (56)
Brown Creeper (87)
Golden-crowned Kinglet (40)
Solitary Vireo (36)
Warbling Vireo (25)
Nashville Warbler (89)
Yellow-rumped Warbler (44)
Hermit Warbler (64)
Western Tanager (71)
Black-headed Grosbeak (61)
FORAGING HEIGHT (meters)
FORAGING HEIGHT (m)
0
10
20
30
-1.0
0.0
+1.0
PREFERENCE VALUES

plants that were seldom used by these birds which primarily occupy forested areas during the breeding season. MacGillivray's Warblers (Oporornis tolmiei) and Wilson Warblers (Wilsonia pusilla) were not included in this analysis due to limited numbers of observations, but were more common in brushfield habitats than were the species considered here.

Secondly, some primarily forest birds from the ground-seed foraging guild were often seen gleaning insects from the lower portions of forest trees. For example, the Dark-eyed Junco (Junco hyemalis), which was the most abundant bird recorded on sample plots, occurred in the lower two layers on 55% of its foraging observations in trees (unpublished data). Thus, the apparent underuse of lower layers by the insect-gleaning guild may have resulted from a depletion of insects by ground foragers.

Only the Nashville Warbler showed a positive preference for the 0.5-2 m layer, using patches of low forest and brush more than other guild members. Since it is the only ground-nester in the guild, its use of brush may relate to the low cover required for nesting (Grinnell and Miller 1944:396).

A final consideration in judging the value of low foliage to the guild is that these observations were taken only during the breeding period. Later in the year when much of the arboreal foliage has matured and presumably produces fewer insects, some species intensify their use of the brush species with softer foliage, especially using Ceonothus integerrimus (unpublished data).

The lack of a strong preference for upper foliage layers by the community as a whole contrasts with Balda's (1969) results from the Chiracahua Mountains in Arizona. However, his analysis included all birds in his study area. It appears that at Blodgett Forest the insectivorous bird community uses all foliage above 2 meters in proportion to its availability, but individual species have specialized by subdividing the vegetation, probably to improve foraging efficiency.

Tree Species

In contrast to the apparent lack of preference for foraging height shown by the 12 birds as a group, the guild did prefer certain tree species for foraging (Figure 3). Ponderosa pine, sugar pine, black oak and white fir were all used significantly more than expected. Incense cedar was used considerably less than expected, while Douglas fir was used in proportion to its availability.

Individually, different birds preferred different tree species for foraging substrates (Figure 4). The strengths of preferences also differed among species. A summary of the preference patterns for each species shows that in 36% of the testable comparisons, tree species use differed significantly from that expected based on relative tree species cover values (Table 1). This summary weights each bird species equally rather than by its relative frequency of occurrence (as in Figure 3), yet the use patterns remain the same among possible comparisons. Thus, unlike vertical foliage structure, where

Figure 3 - Tree species preferences (Ivlev 1961) of the insect-gleaning guild at Blodgett Forest. Utilization (observed proportion) was derived from the observations of tree species use by each bird species weighted by its relative abundance on the forest. Availability (expected proportion) was derived from tree species cover values on all sample plots. Tree species codes are: PIPO = ponderosa pine, PILA = sugar pine, ABCO = white fir, PSME = Douglas fir, LIDE = incense cedar, QUKE = California Black Oak. The comparisons of observed and expected use are significantly different (X^2, 1 d.f., $p < .05$) for each tree species except Douglas fir.

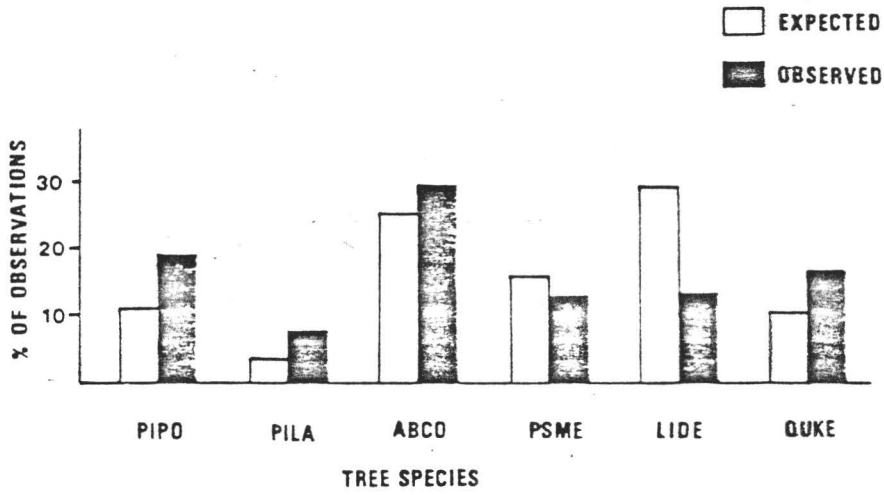

EXPECTED
OBSERVED
% OF OBSERVATIONS
30
20
10
PIPO
PILA
ABCO
PSME
LIDE
QUKE
TREE SPECIES

Figure 4 - Tree species preferences (Ivlev 1961) for each of the 12 insect-gleaning guild members measured during the breeding season. See Figure 3 for tree species codes. Hatched bars are those values for which used and available proportions differed significantly (X^2, 1 d.f., $p < .05$). Numbers of observations are in parentheses.

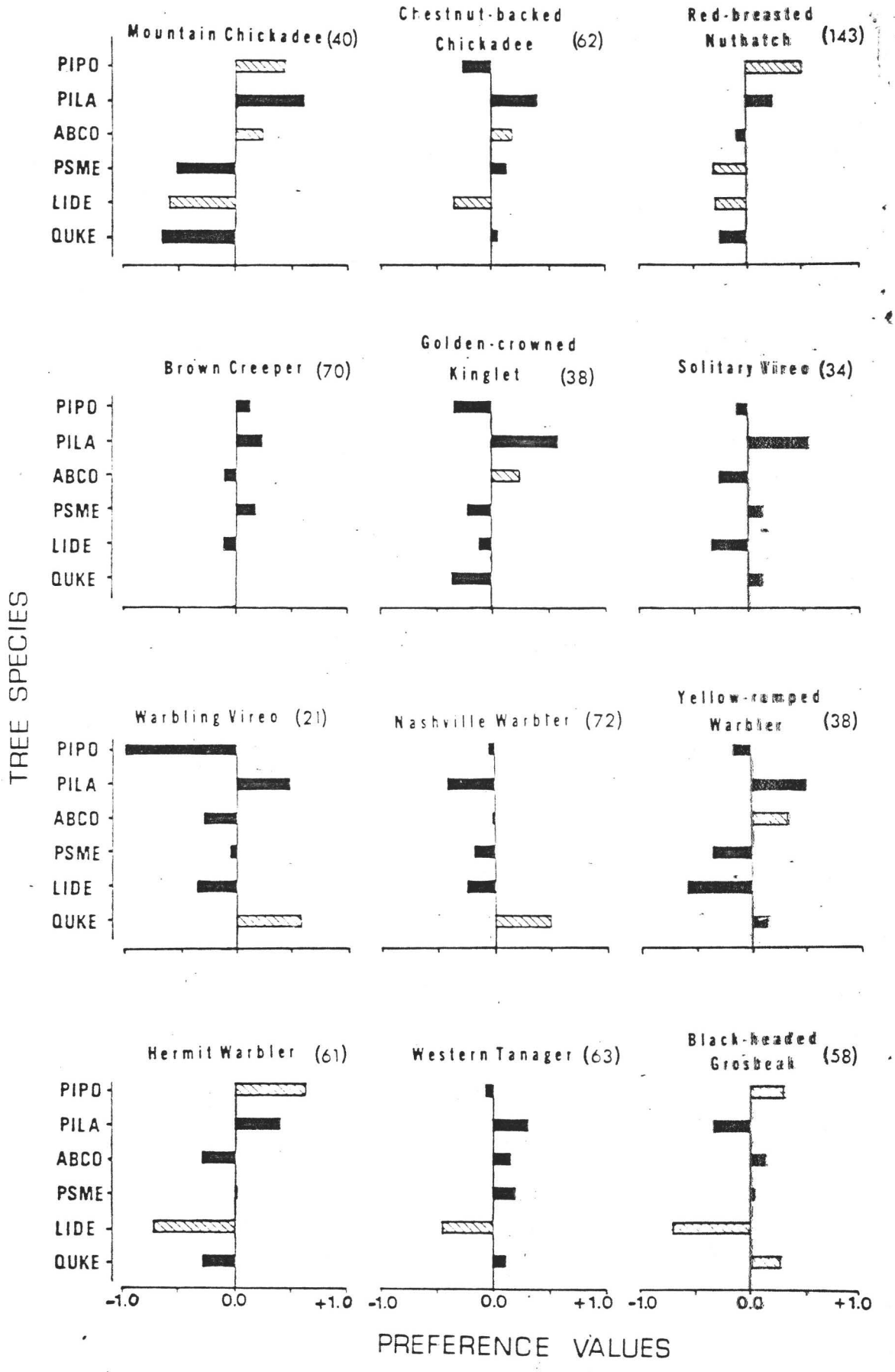

Mountain Chickadee (40)
Chestnut-backed Chickadee (62)
Red-breasted Nuthatch (143)
Brown Creeper (70)
Golden-crowned Kinglet (38)
Solitary Vireo (34)
Warbling Vireo (21)
Nashville Warbler (72)
Yellow-rumped Warbler (38)
Hermit Warbler (61)
Western Tanager (63)
Black-headed Grosbeak (58)
PIPO
PILA
ABCO
PSME
LIDE
QUKE
TREE SPECIES
-1.0
0.0
+1.0
PREFERENCE VALUES

Table 1 - Numbers of bird species showing significant preference for the 6 major tree species. X^2 tests (1 d.f., $p < .05$) were used to evaluate preference. Not testable class are those comparisons for which the expected number of observations were less than 5. Percentages of the total number of testable comparisons are in parentheses.

	PIPO	PILA	ABCO	PSME	LIDE	QUKE	Total
Selection (+)	4	-	4	-	-	3	11 (21)
Avoidance (-)		-	-	1	7	-	8 (15)
Not Significant	4	-	8	10	5	6	33 (64)
							(100)
Not Testable	4	12	-	1	-	3	20
							72

differential specialization occurs among birds, tree species are recognized in a somewhat more consistant way by all species. Notably, in no case is a tree species significantly preferred by one bird and avoided by another. The bird community's preferences for different tree species at Blodgett Forest is consistent with the preferences shown in other forested areas by Gibb (1954), Balda (1969), and Franzreb (1978).

Possible reasons for the selection of certain tree species by foraging birds include: food abundance, food quality, costs of exploitation, as well as protection from predation and inclement weather (Franzreb 1978). I know of no information on the nutritional quality of insects in different trees or at different heights. Because incense cedar has the densest foliage of any of the trees studied at Blodgett, yet is generally avoided, protection does not appear to be a major factor in tree species choice. Four tentative reasons for the great underuse of incense cedar are: (1) cedar's small, scale-like needles may grow to maturity sooner, reducing the period of suseptibility to attack by phytophagus insects and thus lowering insect density; (2) essential oils, which make incense cedar wood resistant to decay (Anderson 1963) and are present in foliage (Zarvarin 1958), may also influence foliage digestibility and thus insect abundance; (3) cedar's greater foliage density or leaf arrangement may hinder bird's foraging movements and their visibility of prey; (4) a good portion of the cover measured for cedar consisted of closely spaced understory trees; therefore, birds may be avoiding it due to its inaccessibility.

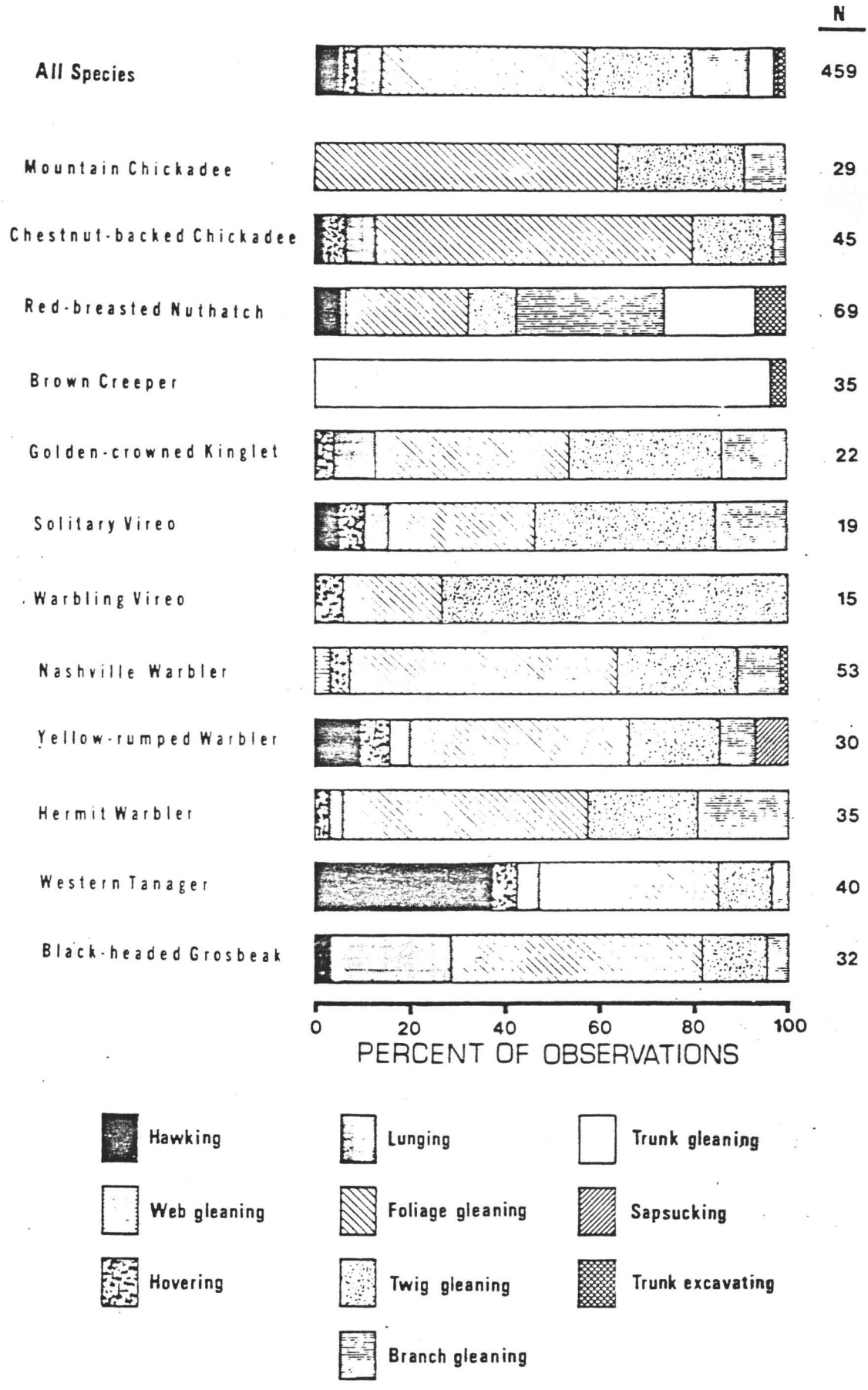
Although little information is available to permit a ranking of the likelihood of the above hypotheses in explaining the underuse of cedar, one inference deserves mention. White fir grows in thick understory stands similar to (and often associated with) incense cedar, yet it shows no dramatic underuse. This suggests that inaccessibility of foliage is not responsible for the low use of cedar. Balda (1969) found similar underuse in Juniperus deppeana, which also has fungus-resistant essential oils and produces dense foliage.

Foraging Behavior

Different foraging behaviors are used disproportionately by the bird community as a whole (Figure 5). Foliage gleaning comprises 44% of all observations, nearly twice that of the next largest category. When foraging behavior is subdivided into its component parts: crown position and technique, the use of crown positions are represented as: outside (aerial) 5%, foliage 51%, twigs 23%, branches 12% and trunks 8%. Considering techniques, gleaning comprised 78% of the observations, while each of the other techniques occurred in less than 5% of the observations.

The use of different foraging tactics permits exploitation of somewhat different insect resources. Hawking and lunging take more active insects (Root 1967), while hovering and gleaning exploits the less active surface insects. Feeding at sapsucker holes, noted only for the Yellow-rumped Warbler, may have resulted in use of insects, sap or both. Although general similarity exists in foraging behaviors

Figure 5 - Foraging behaviors used by the insect-gleaning guild as a whole and by individual species during the breeding season. Numbers of observations are shown to the right of each graph.


N
All Species
459
Mountain Chickadee
29
Chestnut-backed Chickadee
45
Red-breasted Nuthatch
69
Brown Creeper
35
Golden-crowned Kinglet
22
Solitary Vireo
19
Warbling Vireo
15
Nashville Warbler
53
Yellow-rumped Warbler
30
Hermit Warbler
35
Western Tanager
40
Black-headed Grosbeak
32
0
20
40
60
80
100
PERCENT OF OBSERVATIONS
Hawking
Lunging
Trunk gleaning
Web gleaning
Foliage gleaning
Sapsucking
Hovering
Twig gleaning
Trunk excavating
Branch gleaning

used by different species, some notable specializations occurred. Brown Creepers fed exclusively on tree trunks, sharing this location only to a moderate degree with Red-breasted Nuthatches. Western Tanagers were unique in their hawking of insects on many occasions. Black-headed Grosbeaks used lunging considerably more than any other species.

Niche Breadth

A comparison of niche breadths on different axes gives some indication of the degree of specialization occurring on each axis (Table 2). The results show that foraging behaviors are much less diverse than are uses of heights or trees. Only the generalized Red-breasted Nuthatch shows a foraging behavior breadth of a magnitude similar to other axes. Its behavioral diversity is almost twice that of the next most generalized foragers, the Solitary Vireo and Yellow-rumped Warbler.

Variations in the niche breadths along different axes show to what extent the community subdivides the axes. Foraging behavior, with a coefficient of variation (CV) of 0.59, shows much greater variation in diversity of classes used than either foraging height (CV = 0.09) or tree species (CV = 0.14) (Table 2).

The niche breadth values for a species may provide an index to its relative susceptibility to habitat change. For example, the Mountain Chickadee has a 21% higher niche breadth value for foraging height than the Chestnut-backed Chickadee. Hence, changes in foliage profiles through forest management may affect Chestnut-backed

Table 2 - Niche breadth values (Colwell and Futuyma 1971) for foraging heights, tree species and foraging behaviors used by birds.

	Foraging Height	Tree Species	Foraging Behavior
Mountain Chickadee	.84	.66	.27
Chestnut-backed Chickadee	.63	.71	.29
Red-breasted Nuthatch	.76	.77	.78
Brown Creeper	.80	.81	.13
Golden-crowned Kinglet	.63	.62	.38
Solitary Vireo	.71	.96	.43
Warbling Vireo	.70	.68	.15
Nashville Warbler	.82	.76	.37
Yellow-rumped Warbler	.82	.64	.42
Hermit Warbler	.67	.60	.34
Western Tanager	.69	.74	.37
Black-headed Grosbeak	.77	.75	.33
$\bar{X}$	.74	.72	.36
S.D.	.07	.10	.16
C.V.	.09	.14	.59

Chickadees more severely. Unfortunately, the significance of differences in these niche breadth values cannot be tested statistically. For a single species, the particular pattern of potential suseptibility to habitat change is best shown by the preference diagrams (Figures 2 and 4).

Hespenheide (1975) and Levins (1968) have suggested that specialization (low niche breadth) on one axis may result in the use of a wider range of resources on other axes. However, when each species' niche breadth values for different axes were correlated with one another on a pairwise basis, no significant relationship was noted (Table 3). Thus, in this community, the breadth of use of one axis gives little information on patterns of use on others.

Niche Overlap

Values for niche overlap between species for each of the three axes were also calculated by the Colwell-Futuyma method (Table 4). The results show extensive overlap between many species pairs for all three axes, although foraging behavior shows the lowest overlap overall.

Total overlap on the three axes could not be based on the proportions of observations in each combination of the classes on each axis, as in Inger and Colwell (1977), because foraging behavior was recorded in 1978 only. For comparisons of species pairs over the three resource axes, the product of the three individual overlaps ($\cdot\alpha$) is used. The decision to use the product rather than the sum of the individual overlaps was based on the independence of the three overlap measures as determined by a pairwise correlation of overlaps (Table 5), as in

Table 3 - Results of pairwise correlations of niche breadths on the three niche axes. Correlation coefficients (r) and significance values (p) are given.

	Tree Species		Foraging Behavior	
	r	p	r	p
Foraging Height	.07	.41	.17	.30
Tree Species			.30	.18

Table 4 - Overlap values for pairs of species on three niche axis and the product of overlaps. α_h = foraging height overlaps; α_t = tree species overlap; α_f = foraging technique overlap; $\cdot\alpha = (\alpha_h) \times (\alpha_t) \times (\alpha_f)$. Overlap values are scaled to range between 0 and 1 to allow comparison of values on different axis. Mean overlap values on each axis are also presented.

1/ Codes are derived from the first two initials of genus and species name, and are keyed in the vertical axis of the table.

2/ Mean overlaps in foraging techniques are also calculated with the Brown Creeper deleted. Since overlaps for the Creeper and all other species are extremely low on this axis, this value provides a better index for comparison of all other species.

		Paru[1]	Sica	Cefa	Resa	Viso	Vigi	Veru	Deco	Deoc	Pilu	Phme	Mean	
	α_h	.95	.96	.94	.92	.94	.92	.92	.98	.96	.96	.95	.94	
Mountain	α_t	.84	.93	.88	.84	.82	.82	.85	.87	.92	.88	.92	.87	
Chickadee	α_f	.94	.58	.00	.94	.90	.70	.96	.92	.97	.87	.93	.79	(.87)[2]
(Paga)	$\cdot\alpha$	.76	.52	.00	.73	.68	.53	.76	.79	.86	.74	.81	.65	
	α_h		.89	.81	.92	.82	.87	.77	.96	.98	.91	.97	.90	
Chestnut-backed	α_t		.86	.95	.96	.95	.89	.94	.97	.75	.99	.92	.91	
Chickadee	α_f		.56	.00	.92	.89	.64	.92	.96	.94	.97	.95	.79	(.87)
(Paru)	$\cdot\alpha$		.43	.00	.82	.69	.49	.66	.89	.69	.88	.85	.65	
	α_h			.97	.95	.97	.98	.95	.96	.94	.96	.94	.95	
Red-breasted	α_f			.94	.82	.89	.85	.89	.84	.93	.89	.93	.89	
Nuthatch	α_t			.10	.58	.61	.35	.70	.62	.60	.56	.58	.53	(.58)
(Sica)	$\cdot\alpha$			.09	.49	.53	.29	.60	.50	.52	.48	.51	.45	
	α_h				.89	.98	.95	.99	.92	.89	.90	.89	.92	
Brown	α_t				.92	.96	.95	.95	.90	.85	.96	.94	.93	
Creeper	α_f				.00	.00	.00	.07	.00	.00	.00	.00	.02	(n/a)
(Cefa)	$\cdot\alpha$				.00	.00	.00	.07	.00	.00	.00	.00	.01	
	α_h					.91	.97	.87	.95	.97	.98	.96	.94	
Golden-crowned	α_t					.89	.92	.90	.93	.69	.93	.84	.88	
Kinglet	α_f					.96	.75	.93	.92	.98	.88	.92	.80	(.88)
(Resa)	$\cdot\alpha$					.78	.67	.73	.82	.66	.80	.74	.65	
	α_h						.94	.97	.92	.90	.81	.89	.92	
Solitary	α_t						.91	.94	.90	.79	.95	.91	.90	
Vireo	α_f						.76	.89	.95	.94	.88	.89	.79	(.87)
(Viso)	$\cdot\alpha$						.65	.81	.78	.67	.76	.72	.64	
	α_h							.91	.95	.93	.94	.94	.94	
Warbling	α_t							.88	.82	.77	.87	.83	.90	
Vireo	α_f							.70	.66	.70	.59	.60	.59	(.64)
(Vigi)	$\cdot\alpha$							.56	.51	.50	.48	.47	.47	
	α_h								.89	.86	.88	.87	.90	
Nashville	α_t								.92	.76	.95	.93	.90	
Warbler	α_f								.90	.95	.86	.90	.78	(.86)
(Veru)	$\cdot\alpha$								.74	.62	.71	.72	.63	
	α_h									.98	.97	.99	.95	
Yellow-rumped	α_t									.75	.97	.93	.89	
Warbler	α_f									.93	.97	.94	.84	(.93)
(Deco)	$\cdot\alpha$									.68	.91	.88	.68	
	α_h										1.00	.97	.94	
Hermit	α_t										.80	.88	.81	
Warbler	α_f										.88	.92	.80	(.88)
(Deoc)	$\cdot\alpha$										.70	.79	.61	
	α_h											.97	.94	
Western	α_t											.96	.92	
Tanager	α_f											.91	.84	(.92)
(Pilu)	$\cdot\alpha$											.85	.66	
	α_h												.94	
Black-headed	α_t												.91	
Grosbeak	α_f												.77	(.85)
(Phme)	$\cdot\alpha$												.67	

Table 5 - Results of pairwise correlation of birds' foraging niche overlap values on three niche axes. Relationships between overlap values of all pairwise combinations of bird species on each combination of two of the three foraging niche axes were tested.

	Tree Species		Foraging Technique	
	r 1/	p 2/	r	p
Foraging Height	.04	.38	.17	.08
Tree Species			.12	.16

1/ Correlation coefficient

2/ Significance level of slope

Hespenheide (1975). The product is considered to be the best method for combining separate overlaps on different axes when they are independent (Cody 1974, May 1975).

Product α describes the overall resource use overlap between the species considered here. A mean overlap value for each species can be calculated as: $\bar{\alpha} = \sum \alpha_{ij}/n-1$, where α_{ij} is the overlap of each species j with species i, and n is the number of species in the community. The mean overlap is an index of the total amount of community overlap with each species. This measure is analogous to diffuse competition (MacArthur 1972), although at this point it is only analogous since no information is available on the distributions of species along niche axes in the absence of other species (Colwell and Futuyma 1971).

The community overlap measures in Table 4 are not exhaustive measures of overlap of each species with the total bird community, but only with the species considered here and only on three niche axes. Other local species which are recognized as members of other guilds show some overlap with peripheral members of the insect-gleaning guild. For example, Western Tanagers were observed flycatching during 38% of their foraging observations, and would show some niche overlap with the more typical flycatching insectivores: the Western Wood Pewee, (Contopus sordidulus), Olive-sided Flycatcher (Nuttallornis borealis), and Empidonax flycatchers. Similarly, the trunk-using Brown Creeper and Red-breasted Nuthatch would overlap with members of the insect-excavating guild (woodpeckers) which also glean insects from trunks to some extent. But for the majority of the species considered

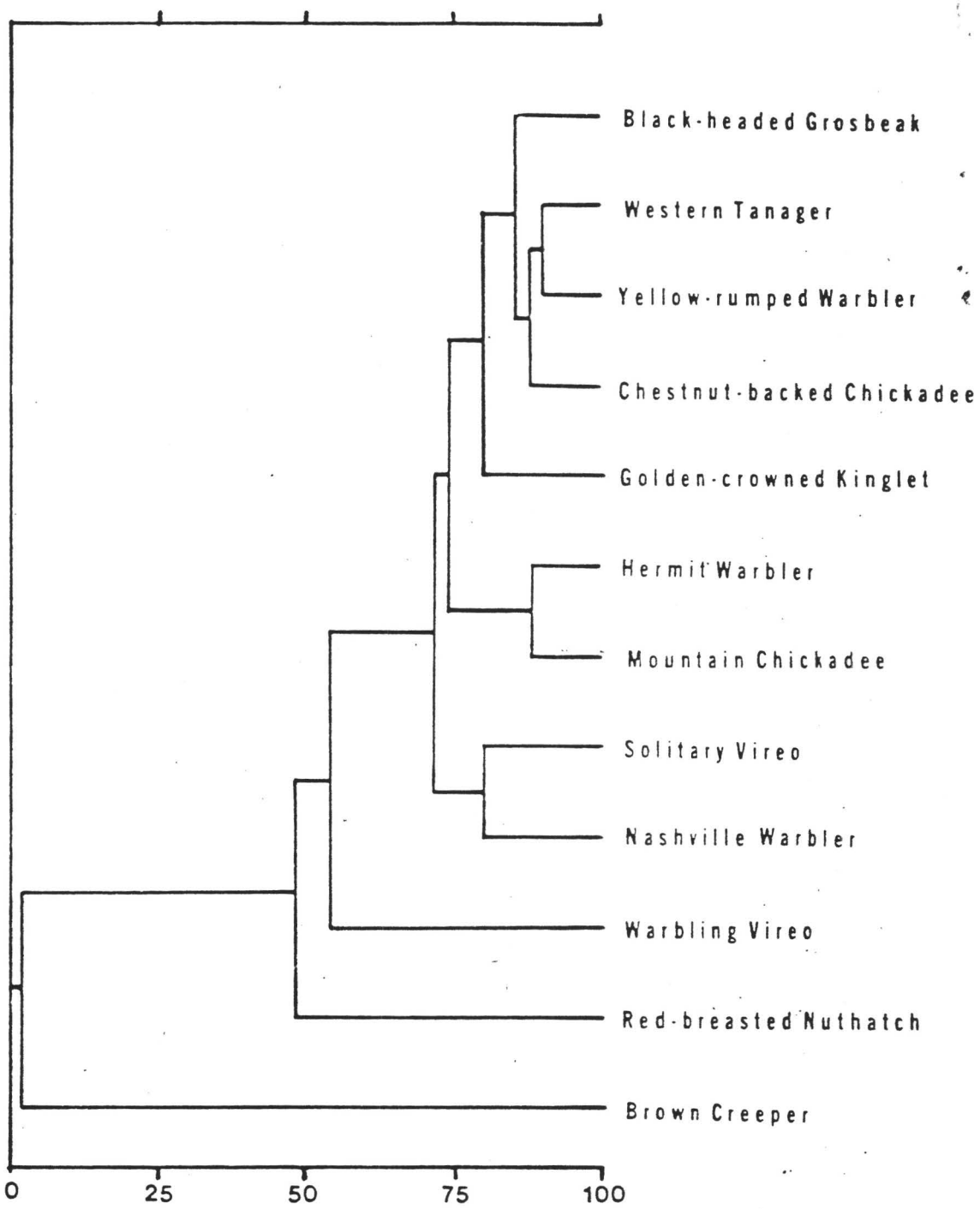
here, overlap with other guilds is slight, and thus $\cdot\bar{\alpha}$ provides a measure of most of the overlap of the whole bird community with each species.

From this discussion, the mean niche overlap values would have been expected to be higher in the Brown Creeper, Red-breasted Nuthatch and Western Tanager if all species had been included. Except for the Warbling Vireo, whose small sample size may have influenced overlap values, the remaining 9 species all show mean overlaps 0.61 to 0.67. That this represents some maximum allowable overlap in these sympatric species is a seductive but unproven possibility.

Similarities in species' foraging niches are displayed in a cluster diagram (Figure 6). Species are clustered on the basis of foraging overlap ($\cdot\alpha$). The more similar species and species groups are clustered toward high values of niche overlap.

A pattern that emerges from the foraging overlap dendrogram is the disjunction in the similarity of most guild members and the three peripheral guild members: the Warbling Vireo, Red-breasted Nuthatch, and Brown Creeper. These three tend to be isolated from all other guild members. The low overlap of the Warbling Vireo is a result of its strong preference for oak (Figure 4) and its specialization on twigs as a foraging substrate (Figure 5). Unfortunately, this divergence may be an artifact of the small number of observations obtained for this relatively uncommon species (n = 15 to 25 for the 3 axes), and inferences drawn for this species must be considered as tentative. The dissimilarity of the Red-breasted Nuthatch is mainly a

Figure 6 - Dendrogram showing similarities in foraging methods used by insect-gleaning birds based on overlap values (Colwell and Futuyma 1971) in Table 4. Product α is the product of overlaps on three niche axes: foraging height (α_h), tree species (α_t), and foraging techniques (α_f).


Black-headed Grosbeak
Western Tanager
Yellow-rumped Warbler
Chestnut-backed Chickadee
Golden-crowned Kinglet
Hermit Warbler
Mountain Chickadee
Solitary Vireo
Nashville Warbler
Warbling Vireo
Red-breasted Nuthatch
Brown Creeper
0
25
50
75
100
% OVERLAP BASED ON FORAGING MEASURES (-alpha)

result of its frequent use of branches and trunks as foraging substrates (Figure 5). The Brown Creeper's exclusive use of trunks (Figure 5) makes it extremely different from all other species in foraging.

Distributional Overlap

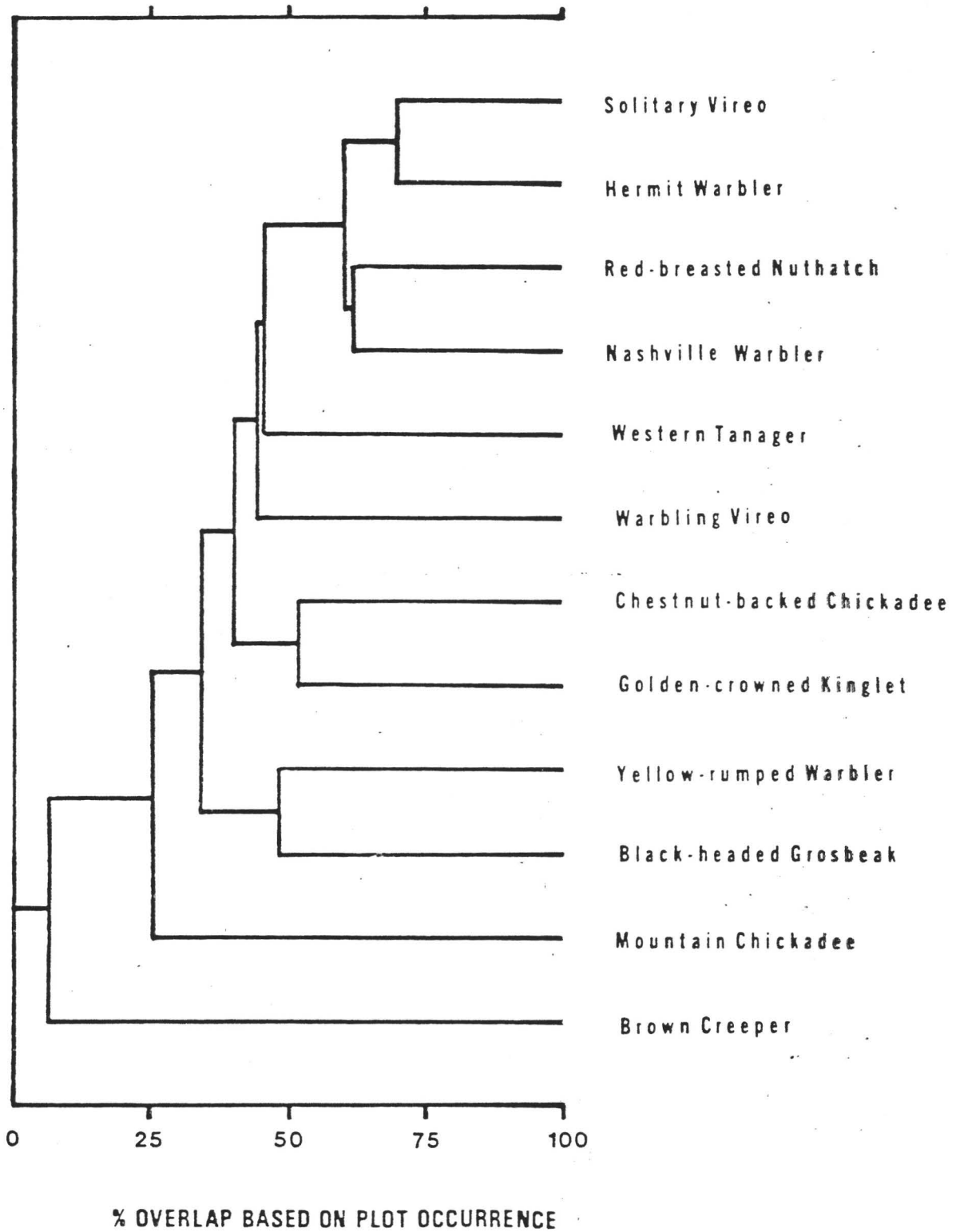
Pairwise overlap values for species' co-occurrence on sample plots measure the degree to which species tended to associate with each other geographically (Table 6). This measure, α_d, is similar to an areal overlap measure (e.g. Cody's habitat overlap, α_h). In Figure 7, species are clustered according to their degree of geographic association during the 1977 breeding season. The absolute magnitude of the co-occurrence values in Figure 7 are not comparable to the foraging overlap values because the intensity of sampling on plots (one morning per plot) undoubtedly resulted in an incomplete census and thus reduced the overall magnitude of the overlaps. Still, the relative similarities of species are probably well described due to the large number of plots sampled.

The dendrogram provides an overview of the similarity of the species' habitat needs. For example, Solitary Vireos and Hermit Warblers tend to occur together most often, and thus have the most similar preferred habitats. Presumably, Brown Creepers and Mountain Chickadees are the most unique in their selected habitats, as shown by their low similarity with the rest of the guild.

Table 6 - Pairwise overlap values (Colwell and Futuyma 1971) for insect-gleaning species based on their frequencies of occurrence on sample plots. Mean overlap values for each species are shown at the right, as an index of habitat specificity. Species codes are as in Table 4.

	Paru	Sica	Cefa	Resa	Viso	Vigi	Veru	Deco	Deoc	Pilu	Phme	Mean Overlap
Mountain Chickadee	.33	.39	.08	.27	.16	.16	.25	.22	.27	.16	.39	.24
Chestnut-backed Chickadee		.56	.07	.51	.42	.39	.33	.37	.53	.32	.38	.37
Red-breasted Nuthatch			.16	.57	.52	.56	.63	.40	.65	.56	.54	.50
Brown Creeper				.10	.00	.00	.12	.29	.21	.29	.23	.14
Golden-crowned Kinglet					.31	.35	.32	.28	.45	.34	.20	.33
Solitary Vireo						.45	.55	.14	.70	.44	.24	.35
Warbling Vireo							.35	.26	.37	.44	.37	.33
Nashville Warbler								.33	.68	.41	.53	.41
Yellow-rumped Warbler									.20	.39	.48	.30
Hermit Warbler										.43	.42	.44
Western Tanager											.40	.39
Black-headed Grosbeak												.38

Figure 7 - Dendrogram showing similarity in geographic association of insect-gleaning birds based on the overlap values (Colwell and Futuyma 1971) in Table 6. Overlaps are based on the frequencies of occurrence of species on sample plots.


Solitary Vireo
Hermit Warbler
Red-breasted Nuthatch
Nashville Warbler
Western Tanager
Warbling Vireo
Chestnut-backed Chickadee
Golden-crowned Kinglet
Yellow-rumped Warbler
Black-headed Grosbeak
Mountain Chickadee
Brown Creeper
0
25
50
75
100
% OVERLAP BASED ON PLOT OCCURRENCE

Foraging and Distributional Overlap

Although the distributional overlaps and diagram (Table 6, Figure 7) show similarities in habitats used by birds, the causes of these similarities do not emerge from such an analysis. Why do some species tend to occur together while others do not? A variety of non-exclusive hypotheses arise to explain this basic ecological question. If resources are abundant, species which forage similarly (use similar heights, trees and behaviors) would be expected to occur in the same locations. However, if resources are limiting, ecological theory predicts that similar species will be repulsed, either through behavioral exclusion (e.g. Davis 1973, Williams and Batzli 1979, and Sherry 1979), or through evolutionary adjustment (morphological and/or behavioral) in which species segregate along certain niche axes to reduce competition (McArthur and Levins 1967).

Finally, co-existing species may have evolved under selective regimes which differed considerably from that imposed by the current environment, including competitors. This process could result in a divergence in habitat requirements that is indistinguishable in pattern from that occurring via behavioral exclusion.

As an example of different possible interpretations of a single distributional pattern, the elevational segregation of Carpodacus finches is instructive. Salt (1952) has demonstrated distinct differences in physiological tolerances of climatic factors among 3 species which presumably result in a distributional segregation that is independent of competition. Cody (1974:17) has proposed competition as potentially responsible. While I feel that Salt's strongly supported

interpretation is superior in this particular example, competitive displacement is still a distinct possibility in local areas and may apply to some of the insect-gleaning species considered here.

Through observation of foraging activities and species distributions, I have shown certain overlap patterns. A comparison of these foraging and distribution overlaps may clarify the role of competition in structuring the breeding bird community. I compared the overall pattern of species' pairwise overlaps on the two axes, specifically testing the null hypothesis that the two overlaps would not be correlated (α unrelated to α_d). Rejection of the null hypothesis could take two forms.

First, a positive correlation should occur when resources are not limiting and similar species could forage together without competing. However, high overlaps in foraging and distribution could also occur if an unmeasured niche axis was being segregated, even when resources were scarce. Species that differed in both foraging methods and preferred habitats would contribute to a positive correlation.

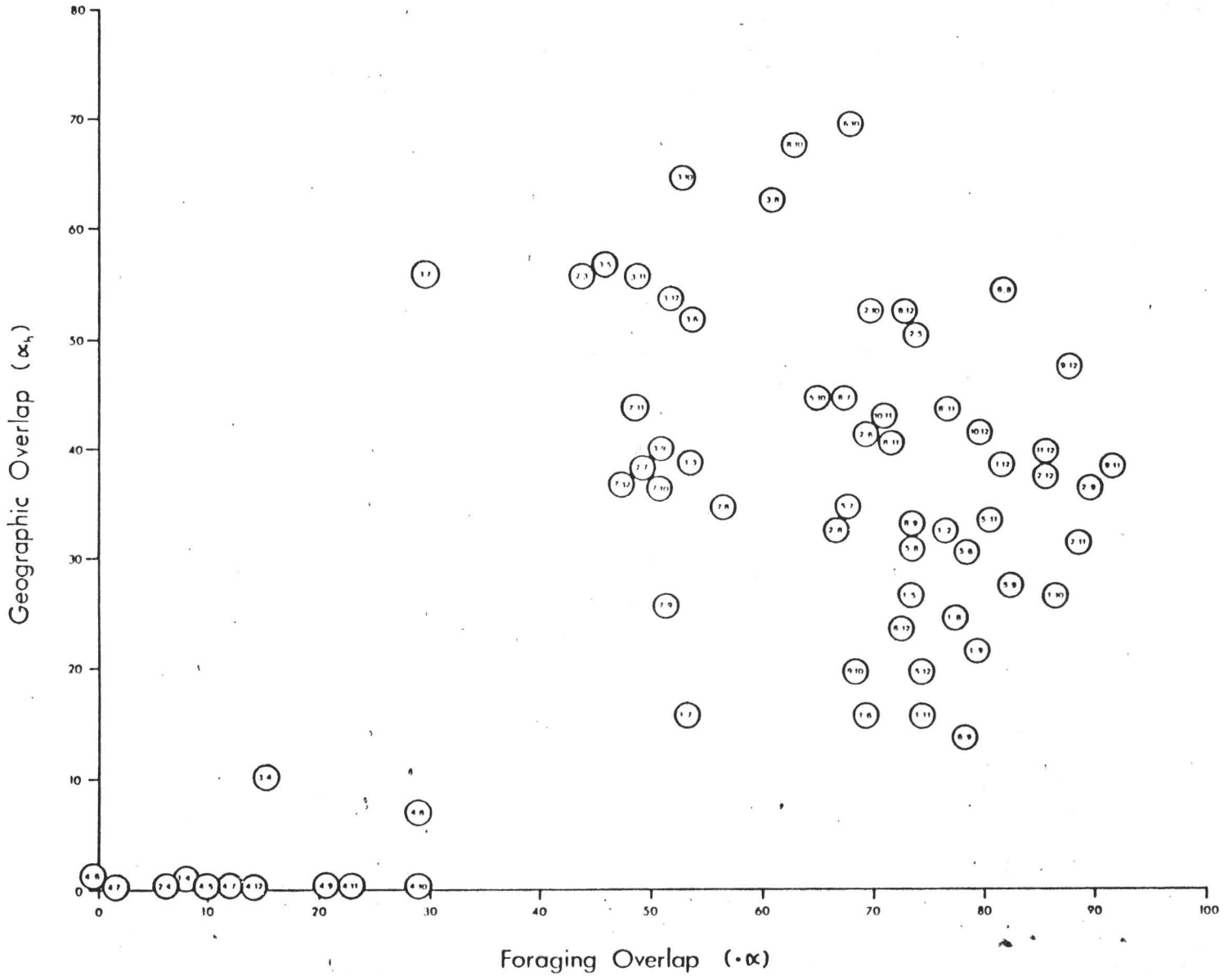
Secondly, a negative correlation should occur where species that forage similarly are forced to occupy different habitats, indicating resource limitation, or where species with different foraging methods prefer similar habitats for different reasons. An inability to reject the null hypothesis would indicate that neither competition nor resource abundance serve as a single overriding factor structuring the insect-gleaning bird community. This result would suggest that the importance of these and other factors may vary depending on the particular set of species considered.

The points indicating overlaps of species pairs on the 2 axes show a wide scatter, so that no significant relationship is described (Figure 8). Thus, the guild appears to be structured by a multiplicity of factors which elude this simple analysis. Still, the overlap relations of particular species may indicate the relative importance of the several environmental and behavioral factors considered. It is likely that species with high foraging overlaps and low distributional overlaps (high $\cdot\alpha$, low α_d) are either selecting different macro-habitat characteristics (e.g. vegetation density), or are segregated as a result of some competitive interaction (either by behavioral interference or through resource exploitation). Species showing low foraging and high distributional overlaps (low $\cdot\alpha$, high α_d) prefer similar areas, but differ in foraging heights, trees or techniques used. This pattern may result from inherent differences in the preferences of the particular species, or through competitive displacement. Those species (epitomized by the Brown Creeper) that show little overlap in either foraging or distribution (low $\cdot\alpha$, low α_d) use different habitats which are exploited in a different manner. Finally, species with high overlaps in both foraging and geographic distribution (high $\cdot\alpha$, high α_d) either may be actually competing, or may be segregating ecologically on the basis of a niche axis not recognized in this study. Species from this latter group are especially deserving of future study.

Figure 8 - Relationship between overlaps in foraging and geographic distribution for each pair of insect-gleaning guild members.

Species codes are as follows:

1 = Mountain Chickadee
2 = Chestnut-backed Chickadee
3 = Red-breasted Nuthatch
4 = Brown Creeper
5 = Golden-crowned Kinglet
6 = Solitary Vireo
7 = Warbling Vireo
8 = Nashville Warbler
9 = Yellow-rumped Warbler
10 = Hermit Warbler
11 = Western Tanager
12 = Black-headed Grosbeak


Geographic Overlap (α_h)
Foraging Overlap ($\cdot\alpha$)
0
10
20
30
40
50
60
70
80
90
100

CONCLUSION

Limitations of the Study

One limitation of this study design is its reliance on a univariate approach. Species may not respond to different resource axis independantly. Rather, the position on one axis may affect the range of choices available on others.

Further, species probably respond to properties of the habitat which cannot be described from simple foraging substrate observations. Requirements for particular vegetation densities, diversities in foliage height (e.g. edge) or diversity of species composition are unobtainable with this method, but may be important in habitat selection and niche differentiation. Further research will provide more information on these complex habitat requirements, and permit testing of hypotheses forumulated in this study.

Due to the amount of effort required, I was unable to sample the basic resource to which the birds are ultimately directed in their specialized foraging patterns: insect distribution and abundance. Thus, reliance on habitat use measures as an index to the ultimate causes of distribution is somewhat suspect. Yet, the consistency of my results with the more anecdotal descriptions of Grinnell and Storer (1924), Bent (1946-1968), and Gaines (1977) suggests that these relationships are of long term duration, and thus serve as accurate indicators of habitat needs in the broad sense. However, more detailed studies of competition and interspecific relations should include surveys of insect food availability and use.

Finally, although evidence for preference of certain resources has been shown in this study, it does not necessarily prove that these preferred resources are critical to the maintenance of populations. Preferences may reflect the species' attempts to increase foraging efficiency, but if other mortality factors are controlling population levels, e.g. overwinter mortality (Fretwell 1972), or nest site availability (Balda 1975), then a decline in the quality of feeding habitat may be relatively unimportant. Preference does not necessarily describe dependence.

Topics for Future Research

Some of the most important questions raised in this study are:

1. How do differences in availability of habitat features (tree species cover and foliage heights) affect the preferences shown by species? A considerable body of literature exists on the changes in prey preferences with variations in prey densities (e.g. Murdoch 1969). Presumably, insectivorous birds form search patterns which improve foraging efficiencies on different types of foliage and different foliage densities. As the abundances of resource substrates change, the value of maintaining various behavioral repertoires should also change, and different preferences should result. These patterns may be evident on a local scale where different combinations of habitat variables are available to different individuals.

2. How do preferences change over time? Although no significant differences in foraging patterns could be shown between the two years in this study, this was probably due in part to small sample sizes. Presumably, insect production varies between seasons and between years in different trees and heights. This variation should also affect the behavioral repertoire and the preference patterns. Furthermore, community relations should change with changes in species composition due to the departure of summer residents, the passage of spring and fall migrants and the arrival of winter residents. Such changes in the guild structure have been shown to alter foraging patterns in other areas (e.g. Herrera 1978).

3. What are the actual bases for the differences in tree species preferences shown by the guild? Two likely hypotheses are: (1) that insect abundance is higher on preferred trees than on avoided trees, or (2) that the efficiency of exploitation of insects varies on different trees, causing preference.

The food abundance hypothesis could be tested by measuring insect abundance on different tree species and comparing with use patterns. The foraging efficiency hypothesis might be tested by comparing the foraging success rates in a species that bill-wipes after a successful foraging encounter (Chestnut-backed Chickadee), with expected rates based on insect abundance on each tree species. The foraging efficiency in different trees could then be evaluated by comparing the relative rates of capture to insect densities on different tree species.

4. To what degree are the niche breadths of the different species a property of the variability within all individuals, or the product of a differentially specialized set of individuals (Van Valen 1965, Hespenheide 1973, 1975)? That is, does a large niche breadth reflects a requirement for habitat or behavioral diversity by the species, or perhaps a tolerance of variation in habitat characteristics by different individuals. Such results have important consequences for management since the first situation would actually describe a specialized animal which requires variability in its habitat, while the second describes a generalist, which may adapt to a variety of habitat conditions. Future studies incorporating experimental manipulation of habitat variables (e.g. removal of one tree species) may shed light on these questions.

5. What are the effects of macro-habitat characteristics, such as vegetation density and patchiness, in influencing habitat selection in this community. These relationships do not emerge from foraging substrate data, but have been shown to be important in habitat selection by birds in many communities (e.g. James 1971, Willson 1974 and Roth 1976). Further multivariate analysis of bird abundance compared with vegetation measures taken on sample plots will address this question.

6. Finally, what are the effects of non-foraging needs on habitat selection? Requirements such as song posts, nest sites and cover (for escape and thermoregulation) probably play important roles in defining habitat suitability and community relations and may be more important limiting factors than food.

Management Applications

Preference compares the use of resources with their availability. By providing an index to the importance of resources, it may suggest potential effects of resource manipulation on bird species. Some examples of these predictions are given below.

Since the use of clearcutting and seed tree methods of even-aged silviculture tends to favor shade intolerant trees such as ponderosa pine, sugar pine and Douglas fir, birds that show strong preferences for these (e.g. Red-breasted Nuthatch and Hermit Warbler) might be expected to increase under these management regimes. Birds that prefer the shade tolerant white fir (e.g. Chestnut-backed Chickadee, Golden-crowned Kinglet and Yellow-rumped Warbler) may be reduced by such systems, but favored by individual tree selection and shelterwood methods. The increasingly common practice of removing the less commercially valuable hardwoods, such as black oak, may have negative effects on Warbling Vireos, Nashville Warblers and Black-headed Grosbeaks.

The Mountain Chickadee shows preferences for both tolerant and intolerant tree species and presumably may be maintained in a wider variety of management regimes if other habitat elements are suitable. Apparently, this species responds more to vegetation density, selecting areas with sparse overstory vegetation (unpublished data). The Brown Creeper, Solitary Vireo and Western Tanager show no tree species preferences and would not be expected to respond to a change in species composition per se.

Since incense cedar was not selected by any species and avoided by many, its reduction may be beneficial to insect-gleaning birds.

With regard to foliage heights, species with preferences for the tallest foliage classes (e.g. Yellow-rumped warblers, Black-headed Grosbeaks, Mountain and Chestnut-backed Chickadees, and Hermit Warblers) could decline with the harvesting of larger trees and intensified management using shorter rotation periods.

Unfortunately, preference for lower foliage layers does not necessarily predict the effect on birds of changes in these layers. Species showing preferences for lower foliage may be favoring one or both of two possible situations: (1) the understory in taller forests, or (2) the overstory in patches with low canopy height. The Brown Creeper, Red-breasted Nuthatch and Vireos are probably examples of the former; the Nashville Warbler is an example of the latter, often occurring in the overstories of shorter stands.

SUMMARY

Twelve avian members of the insect-gleaning guild in a Sierra Nevada mixed conifer-oak forest were studied to determine foraging relations of the bird species and their habitats, and relations between the different bird species in their foraging patterns. Detailed habitat measures on 41 plots were used to describe the foliage available to birds by tree species and height class. This availability was compared to proportions used by birds to determine preferences for various substrates. Comparisons showed that the guild as a whole tended to use foliage height classes in proportion to their availability, yet were strongly selective of trees, preferring pine, oak, and to a lesser extent fir, but greatly underusing incense-cedar. On an individual basis, many but not all bird species tended to specialize on particular trees and foliage heights, but often differed from one another in the substrates selected.

Within-guild comparisons of the birds showed that foliage heights, tree species and foraging techniques (crown position and tactics) all contributed to the ecological segregations of birds, but standardized niche breadth and overlap comparisons showed techniques to be the most important. Comparisons of niche overlaps on all axes were accomplished using the product of the overlaps on individual axes, since they were determined to be independent by correlation analysis. Cluster analysis of the overlap products displayed the

overall foraging relations between species, and suggested subgroupings within the guild. Cluster analysis of pairwise overlaps in frequency of occurrence on census plots provided a graphic representation of distributional relationships which presumably reflected the similarity in preferred habitats of species. Correlations of overlaps in foraging behaviors and distribution, showed no distinct relationship between the two factors. Thus, no dominating role could be shown for competition in structuring relations of the community as a whole. However, in terms of individual species comparisons, the relative magnitudes of the two overlap values show specific patterns of ecological segregation and suggest the relative potential for competition between species.

Possible impacts of various silvicultural practices, each of which tend to favor particular tree species and alter canopy height, were projected from preference relationships. One notable suggestion, is that the reduction in amounts of incense cedar, which at present is artificially high due to fire protection, may benefit this community since 8 of 12 species underused this tree.

Suggestions for future research include an intensified program of insect sampling and bird food habits to determine possible causes of the preferences observed in this study. Determinations of the influence of variations in resource availabilities and guild composition on preferences are needed. Finally, the role of macro-habitat variables and non-foraging needs should supplement the results presented here to more fully describe community needs and relationships.

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